A framework for estimating species-specific contributions to community indicators

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ABSTRACT

Community Weighted Means (CWM) are valuable tools describing community composition with respect to one given trait. They have been widely used as indicators in global change studies to measure biodiversity responses to environmental perturbations. However, how individual species contribute to such community indicators has hardly been investigated. One of the reasons lies in the absence of a methodological framework relating changes in community dynamics to species-specific population variations. Here, we present a comprehensive framework allowing a finer interpretation of changes in CWM, and we propose a way to compute species contributions to these indicators.

We present an analytical framework allowing the quantification of species-specific contributions to changes in the mean (CWM) and the variance (Community Weighted Variance, CWV) of trait distributions in species assemblages monitored through time and space. We apply this approach to a case study investigating the impact of climate change on common bird assemblages in the French Mediterranean area between 2001 and 2012.

This approach allows us to identify that a small proportion of the species drive the changes observed at the community level indicator, and allows the identification of those species. Moreover, we show that the species-specific contributions are not homogeneous between taxonomic groups and that migratory species tend to have a higher impact.

This novel decomposition and interpretation of Community Weighted Means and Variances (for which specific software package is provided along with this article) sheds new light on the drivers of community modifications in response to environmental changes across time and space. Moreover, it represents a relevant and simple way to assess particular aspects of species-specific responses to environmental changes and it is straightforward to use for widely used ecological data on any species group.

1. Introduction

Community ecologists have faced the dilemma of either aggregating complex information using meaningful indices (such as species richness, diversity indices (McGill et al., 2015) or more elaborate indices of community composition (Kampichler et al., 2012) or working on single species information (e.g Julliard et al., 2003; Inger et al., 2015). A consequence of the segregation between these two levels of organisation—community and species—is the difficulty in identifying which species contribute to changes in community diversity and composition. Conversely, studying individual species responses to environmental changes may not allow scaling up to community level responses, in particular because of the importance of species interactions.

The challenge of linking community changes with individual species dynamics has contributed to divide empirical and conceptual global change studies in two main branches. On the one hand, community-level approaches have explicitly focused on describing spatial and temporal trends in diversity and composition. Species richness or diversity indices are often used as integrative descriptors of the community changes (Mackey and Currie, 2001) because community structure and composition are expected to change depending on community assembly rules (Logue et al., 2011). On the other hand, species-level approaches have broadly focused on how individual species occurrences or abundances are distributed along environmental gradients.

Following a disturbance, species abundances and distributions are expected to be altered according to the position and breadth of the species' niche. For instance, if a set of species of interest are tracking the climate according to their specific temperature preferences, climate change is expected to trigger range shifts in their distributions (Thomas et al., 2004).

While these two approaches have independently contributed to better descriptions of biodiversity responses to environmental changes, linking population and community-level dynamics remains a challenge (Walther et al., 2002). This limit was emphasized by a call for adopting a more functional view of community ecology, which would better describe how communities are shaped by explicit environmental gradients and clarify the role of species traits (McGill et al., 2006). To overcome these limits, two methodological approaches providing a description of community responses using functional traits rather than species identity have been recently developed. A first available approach integrating trait variability within communities consists of defining communities' functional structure as the distribution of individuals in a multivariate functional trait space (such a space for plants could be defined by maximum height, rooting depth and leaf area for instance, the values can be averaged by species or taxa, or come from individual sampling when available). The use of this multidimensional functional space based on species traits has emerged as a useful way to quantify expected changes in community structure following environmental changes (Mouillot et al., 2013). Another approach consists of using Community Weighted Means (hereafter, CWM) to describe community composition with respect to one given species-specific trait. CWM have been widely used in global change studies as indicators measuring community reshuffling in response to environmental perturbations. In global change ecology, this approach has been applied to a variety of traits, such as the mean of the realized thermal niche (Community Thermal Index) (Devictor et al., 2008b, 2012; Princé and Zuckerberg, 2015; Clavero et al., 2011; Godet et al., 2011; Jiguet et al., 2011; Kampichler et al., 2012; Lindstrúm et al., 2013; Barnagaud et al., 2012a, 2013; Roth et al., 2014), the Mean Catch Temperature (Cheung et al., 2013), the community weighted latitude (Dulvy et al., 2008), altitude (Clavero et al., 2011), habitat specialization (Clavel et al., 2010) or Ellenberg averaged values (Lenoir et al., 2013). CWM approach has been used on birds (Devictor et al., 2008b; Princé and Zuckerberg, 2015), butterflies (Roth et al., 2014; Devictor et al., 2012), plants (Lenoir et al., 2013) and fish (Dulvy et al., 2008; Cheung et al., 2013) communities. Additionally the community-weighted variance (CWV), defined as the trait variability of a given assemblage, have been used to assess functional diversity (Sonnier et al., 2010; Morin et al., 2014; Chollet et al., 2014; Hulshof et al., 2013; Bernard-Verdier et al., 2012b; Siefert et al., 2015).

Although these two approaches are clearly useful to describe general changes in species assemblages, they still mask underlying species-specific dynamics. In particular, a change in CWM does not tell which species and trait values have been lost or gained and whether the change is driven by a few key species or by the entire species pool. Moreover, integrating inter- versus intra-species variability is not explicitly considered: both CWM and multidimensional approaches generally consider only one averaged trait value per species, ignoring the fact that two individuals of the same species can have different values for the same trait. Accounting for intra-species variability in the trait considered could be central to the understanding of assembly processes (Violle et al., 2012).

Thus, a simple framework allowing the monitoring of changes in community and species dynamics while accounting for functional differences between and within species is missing. While approaches to link species demography to community dynamics already exists (Princé and Zuckerberg, 2015; Tayleur et al., 2016), a simple framework allowing the monitoring of changes in community and species dynamics while accounting for functional differences between and within species is missing. Estimating the contribution of each individual species to

community changes would shed a new light on the processes underlying community reshuffling in response to particular environmental changes. Conservation implications may be very different if only two or three focal species are responsible for an observed change in a community-based index than if the community responded homogeneously. Furthermore, assessing the contributions for meaningful functional groups (e.g. protected or unprotected, competitive or not, exotic or resident) might be of interest to test specific autoecological predictions or to help designing conservation plans.

Here, we propose a general framework, along with open source code, to assess the contributions of species or group of species to CWM variations. We expand this framework to the community-weighted variance (CWV). Finally, we present an application of this method to the French breeding bird survey using a well know indicator, the Community Temperature Index (Devictor et al., 2008b).

2. Partition of Community Weighted Mean variations

2.1. An interaction milieu descriptor

A Community Weighted Mean is the average of the local distribution of a trait in a community (i.e. the expected value of the trait if we take an individual at random from the community: it can be described as the mean field estimator of the trait distribution). Consider a community of R species that was sampled at T different times, with p_{ij} the relative abundance of the $i-th$ species at time t_j, and θ_i the $i-th$ species' mean trait value. The CWM at time t_j is defined by:

$$CWM_j := \sum_{i=1}^{R} p_{ij}\theta_i$$

(1)

CWM are community functional parameters (i.e. aggregated indicators obtained from population level information, as defined in Violle et al. (2007)). They can be seen as the simplest summary statistics of the 'interaction milieu', defined as the pool of local strategies co-occurring in a given assemblage (McGill et al., 2006). For instance, a CWM built from plant height is a descriptor of the mean light-harvesting strategy in this community. CWM are by construction not expected to depend on species richness. Their simplicity (due to the use of a single trait) allows for straightforward biological interpretations at the community scale. CWM exhibit directional changes following a change in the relative proportion of high and low values of the trait considered. For instance, following changes in light availability, the CWM built upon plant height is expected to increase if taller species increase in proportion within the assemblage.

By construction, a change in CWM is silent about species-specific dynamics. Following our example, the increase in the plant height CWM does not inform about whether such an increase is due to an increased proportion of a few of the tallest plants species or a collapse of small plants species composing the community. In other words, CWM are information-poor (i.e. incomplete) descriptors of trait values distributions.

2.2. Species contributions to CWM

The lack of a reliable way to quantify species contributions to a CWM trend (Jiguet et al., 2011; Davey et al., 2013) has limited the practical relevance and implementation of those indices since most conservation plans are based on species-specific measures. Recently, Princé and Zuckerberg (2015) then Tayleur et al. (2016) proposed a way to estimate species contributions to a CWM trend. This statistical approach was inspired by a species jackknife method previously used on diversity indices (Davey et al., 2013). A 'species contribution' quantifies to what extent a species contributes to the general trends observed at the community level. A positively contributing species tends to increase the CWM along the considered time frame whereas a

negatively contributing species tends to decrease it. Although this method has been valuably used to assess specific contributions to CWM changes, its interpretation remained elusive. Indeed, this method does not disentangle the influence of trait values from the population dynamics in the final contribution estimates. To date, the absence of any mathematical formalization of species contributions has prevented a clear quantification of its drivers -and their interactions- on community dynamics.

We argue that a straightforward, mathematically resolved method of species contributions calculation and of their properties would provide information about the factors influencing changes in CWM and contribute to stronger interpretations than statistical observations and jackknife approaches.

Let us measure the slope of a linear fit of CWM timeseries on both the whole dataset (β) and on the whole dataset but the focal species k ($\beta_{\neg k}$). The contribution C_k of a species k is then defined as the difference between these two slopes (Princé and Zuckerberg, 2015):

$$C_k = \beta_{\neg k} - \beta \tag{2}$$

If the trends β are approximated by an obtained least square regression of the CWM index as a function of time, because of the linear nature of the CWM with respect to the trend in relative abundance (see supporting information for a demonstration), this expression can be computed as:

$$C_k = \underbrace{\left[\left(\frac{1}{R-1}\sum_{i=1, i\neq k}^{R}\theta_i\right) - \theta_k\right]}_{\text{Trait originality of species } k} \times \underbrace{\frac{1}{(T-1)Var(\overrightarrow{t})}\sum_{j=1}^{T}p_{kj}\left(t_j - \bar{t}\right)}_{\text{Relative abundance trend of species } k} \tag{3}$$

Expression 3 highlights that species that are the more original in their trait value compared to the rest of the community, or the ones that have a large fluctuation in relative abundance will contribute more to the community change (in term of magnitude of contribution $|C_k|$). Furthermore, positive contributors to the CWM trend are species for whom the relative abundance trend and originality have the same sign. Conversely, negative contributors are species for which those quantities are of opposite sign. Going back to our example where CWM is applied to plant communities and the trait considered is plant height, calculating species contributions using expression 3 reveals which species is contributing in which way to the change in average height: for instance, an exceptionally tall species that is slightly increasing in proportion or a group of slightly smaller-than-average species that are disappearing will both exhibit positive contribution values.

We are now going to propose a slight modification to this expression for the species contribution that we note C_k^*:

$$C_k^* = \underbrace{(\theta_k - \bar{\theta})}_{\text{trait originality}} \times \underbrace{\frac{Cov(\overrightarrow{t}, \overrightarrow{p_{k\bullet}})}{Var(t)}}_{\text{Variation in relative abundance}}\left(t_T - t_0\right)$$

where $\overrightarrow{t}$ is the vector of measurement times and $\overrightarrow{p_{k\bullet}}$ is the vector of relative abundances of the $k - $th species for all measurement times. With this reformulation, we can show that the sum of the species contributions is now exactly the CWM variation as computed by a linear model fitted by ordinary least squares (see supporting information for a demonstration), i.e.:

$$\sum_{k=1}^{R} C_k^* = \left(t_T - t_0\right)\beta \tag{4}$$

This allows for decompositions of the CWM variation according to, for instance, taxonomic or functional groups of species by summing individual contributions. As an example, if A is a given subset of species, we have:

$$\sum_{k\in A} C_k^* + \sum_{k\notin A} C_k^* = \left(t_T - t_0\right)\beta \tag{5}$$

Using this approach and following our example of plant size-based CWM, one could segregate the particular contribution of C4 plants for instance. These first results establish that trends in CWM that are traditionally used to assess changes in community composition through space and time can be easily coupled with an exact and relatively simple calculation of each species-specific contribution or the contribution of groups of species. However, this information does not reveal possible changes in the variability of the trait. To do so, in the following, we propose to extend this framework to the Community Weighted Variance as an informative and complementary metric.

3. Community weighted variances

3.1. CWV as a diversity index

In the following, we go one step further and extend our approach to the community weighted variance (CWV, Sonnier et al., 2010), and we propose a way to compute species contributions to its variations. This extension of the community weighted indices to variance is motivated by the need for a diversity index that is simple to compute and interpret, and complementary to the CWM. Consider a community of R species that was sampled at T different times, with p_{ij} the relative abundance of the $i - $th species at time t_j, and θ_i the $i - $th species' mean trait value. The CWV at time t_j is defined by:

$$CWV_j := \left(\sum_{i=1}^{R} p_{ij}\theta_i^2\right) - CWM_j^2 \tag{6}$$

For a given trait, the CWV is a measure of the mean squared functional originality. An increase in CWV indicates that the community is enriched in original individuals (i.e. of species whose traits have higher or lower values than the trait average). Conversely, a decrease in CWV corresponds to a loss of original individuals. Following our plant example, such an index would allow addressing the question of whether there is a homogenization in plant height in the community. Note that the CWV takes into account the relative species abundances as opposed to the local inter-species trait variance that has been used in some previous studies (Roth et al., 2014). As a result, it gives a more accurate image of the functional diversity in highly uneven communities. Variations of CWM and CWV have generally been considered as independent descriptors of community dynamics. Here we propose a novel, joint analysis of CWV and CWM dynamics allowing a finer interpretation of community dynamics (Fig. 1).

If an increase in CWM is linked to an increase in CWV (Fig. 1, top left), it means that the variation in CWM is due to an increased relative abundance in the community of species that have a higher trait value (or an invasion of new high-valued species).

Conversely, if CWV decreases (Fig. 1, bottom left), it means that the increase in the mean is driven by losses in species with a lower trait value. Thus, a correlation between CWM and CWV means that variations in the mean are due to original individuals, whereas an anti-correlation means that this variation is due to unoriginal individuals.

3.2. Species contributions to CWV

Similarly to the CWM, we propose a decomposition of a CWV variation that can be used to distinguish the relative contributions of species, or groups of species, to the variation in the indices:

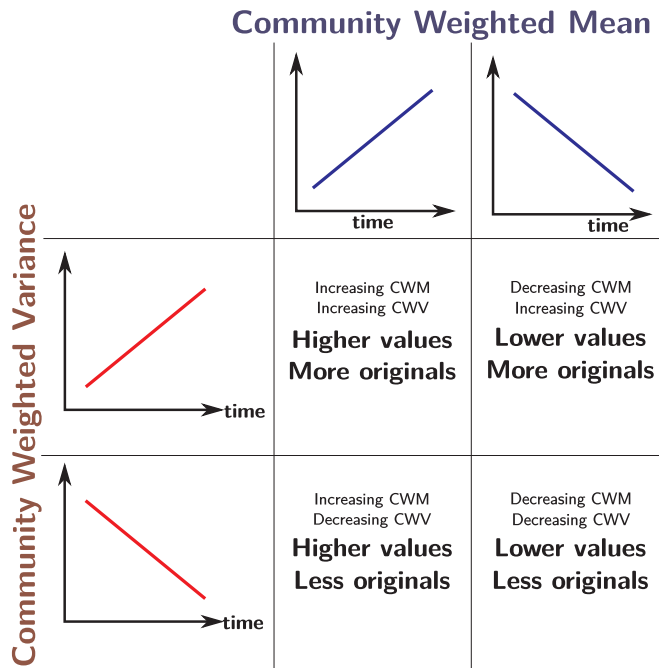$$\Delta CWV = \sum_{k=1}^{R} \mathscr{C}_k \tag{7}$$

with:

Community Weighted Mean

	Increasing CWM	Decreasing CWM
	Increasing CWM Increasing CWV **Higher values** **More originals**	Decreasing CWM Increasing CWV **Lower values** **More originals**
	Increasing CWM Decreasing CWV **Higher values** **Less originals**	Decreasing CWM Decreasing CWV **Lower values** **Less originals**

Fig. 1. Community weighted indices variations provide simple heuristics to understand functional changes in communities. The Community Weighted Mean gives indication about the change in trait toward higher or lower values, the community weighted variance informs about the trait-originality of the individuals. Both variations can be analysed further by a decomposition in the contribution of each species.

$$\mathscr{C}_k = \underbrace{(\theta_k^2 - \overline{\theta^2})}_{\text{Squared-trait originality}} \times \underbrace{\frac{Cov(\vec{t}, \overrightarrow{p_{k\bullet}})}{Var(\vec{t})}\left(t_T - t_0\right)}_{\text{Variation in relative abundance}} - \underbrace{H}_{\text{Constant for all } k}$$

where $\overline{\theta^2} := \frac{1}{R}\sum_{k=1}^{R}\theta_k^2$ is the average squared-trait. Please see the Supporting information for a demonstration and the expression of the constant H.

In the same way as for the CWM, the computation of species (or group of species) contributions is straightforward. It directly reveals

which individual species contribute to the increase or decrease of community homogeneity.

Note that this definition of the CWV only takes into account the relative abundances of species. Taking into account the global population size can be done by dividing the value of the *CWM* by the number of individuals $\frac{1}{N}$ (or $\frac{1}{N-1}$ if using Bessel's correction for small samples). In the following, we only consider relative abundances, assuming that the population size is constant through time. Population size cannot be ignored when it differs between communities under comparison, but this goes beyond the scope of this manuscript.

3.3. Taking intra-specific variation of a trait into account

All the individuals of a given species are not perfect clones, some traits (such as size or diet specialization) can exhibit non-negligible intra-species variability (Albert, 2015; Albert et al., 2012). If we only know the intraspecific variance of the trait (noted σ_i^2 for the $i-$th species), a reasonable assumption is to consider that it follows a normal distribution with mean θ_i and variance σ_i^2. Our approach can be easily generalized to take into account this information when available. Firstly, the CWM is not affected by the addition of the variance of the trait: it stays the same regardless of intra-specific variation (a consequence of its linearity). However, the CWV expression will be different since intraspecific trait variation increases the community wide variance. Consequently, the community distribution of the trait is a Gaussian mixture and its variance is given by Frühwirth-Schnatter (2006):

$$CWV_j = \left[\sum_{i=1}^{R} p_{ij}\left(\sigma_i^2 + \theta_i^2\right)\right] - CWM_j^2 \tag{8}$$

We note $\Theta_k := \theta_k^2 + \sigma_k^2$ for all $k = 1, 2...R$ and $\bar{\Theta} := \frac{1}{R}\sum_{i=1}^{R}\Theta_i$ their average. The expression of species contributions becomes:

$$\mathscr{C}_k = \underbrace{(\Theta_k - \overline{\Theta_k})}_{\text{Squared-trait originality}} \times \underbrace{\frac{Cov(\vec{t}, \overrightarrow{p_{k\bullet}})}{Var(\vec{t})}\left(t_T - t_0\right)}_{\text{Variation in relative abundance}} - \underbrace{H}_{\text{Constant for all } k}$$

This, however, requires knowing trait values at the individual rather than at the species level, and will not be illustrated in our case study because of the lack of relevant data. However, accounting for intra-
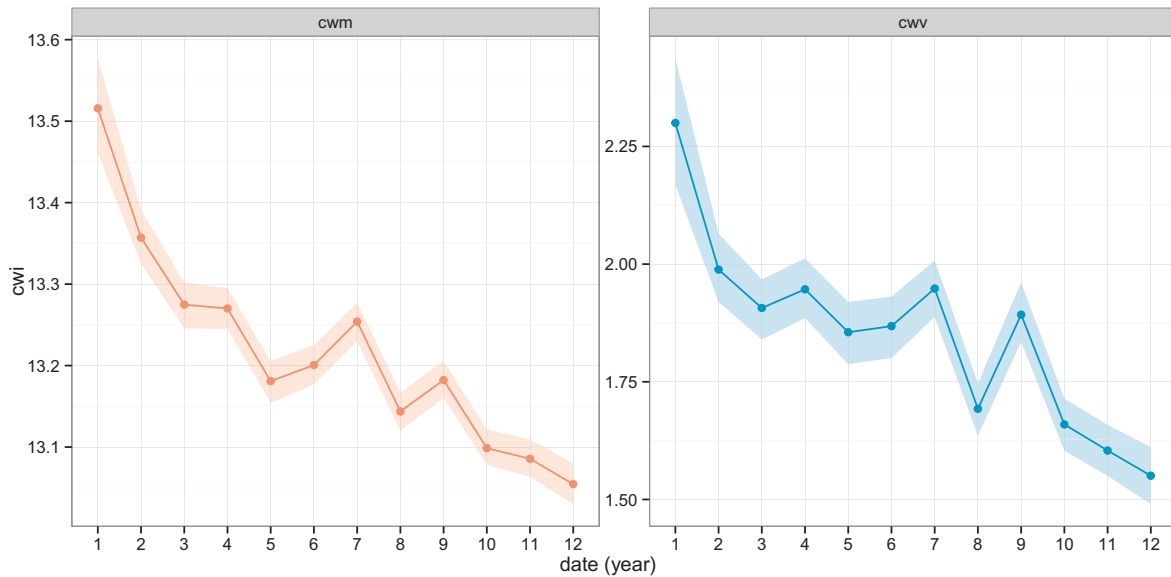

Fig. 2. Annual values (2001–2012) of French Mediterranean Bird Communities Weighted Mean (left) and Variance (right) of STI. Shaded areas are 90% bootstrap confidence intervals.
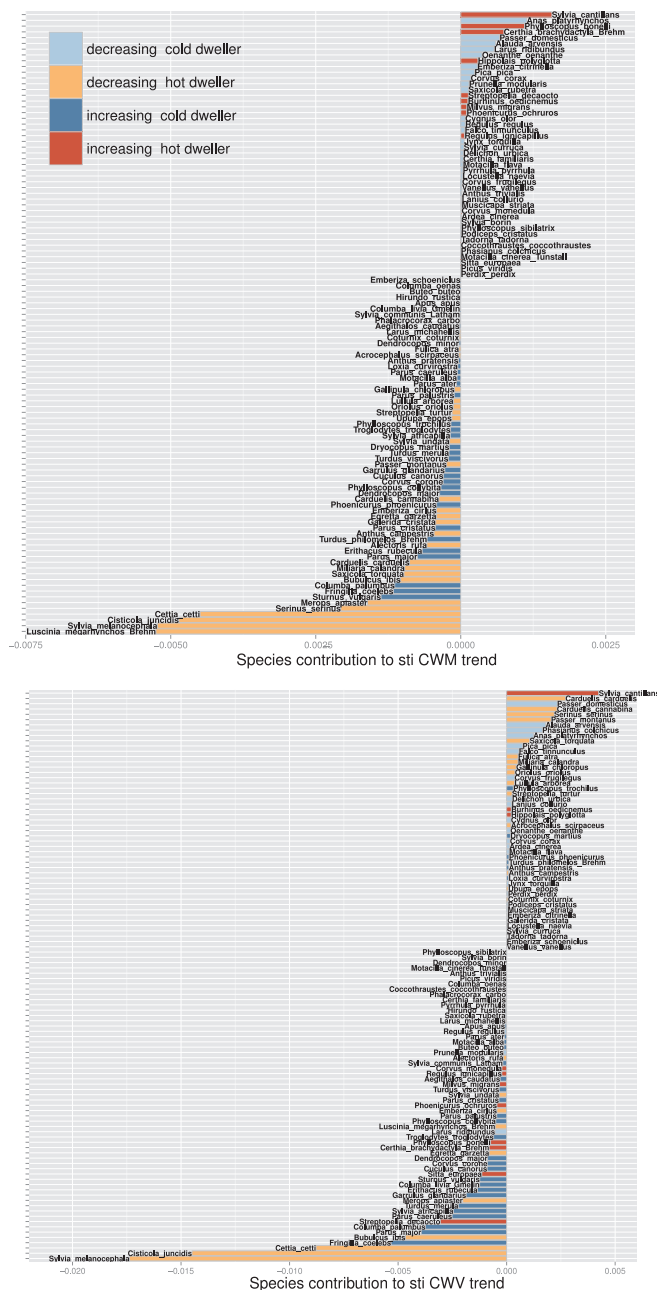
Fig. 3. Species contribution of French Mediterranean Bird Communities Weighted Mean (upper panel) and Variance (lower panel) of STI for the period 2001–2012. Bar colors indicate the interaction between species population trend and STI value (cold dweller = low STI value, hot dweller = high STI value).

specific variation of traits can be of critical interest (Violle et al., 2012). For instance, diet specialization was shown to be highly variable among individuals of a given species and this information can be integrated to further test the importance of intra and inter species contribution (Bolnick et al., 2003, 2011).

4. Case study: community reshuffling of French Mediterranean bird assemblages

4.1. Objectives and dataset

To investigate the informative power of the approach described in the previous sections, we applied our framework to the Mediterranean

avifauna monitored by the French Breeding Bird Survey (FBBS) between 2001 and 2012 (Julliard et al., 2006) and described community changes in regard to a particular trait reflecting the thermal preferences of species. Note that our study is very similar to many studies based on large scale monitoring of biodiversity (Pereira and David Cooper, 2006). Our method is therefore relevant to any large scale survey in which assemblages of specifics groups are monitored in space and time. We (i) studied the interrelation between CWMs and CWVs trends to understand which particular dynamics of species are shaping community changes. We also aimed at (ii) identifying the species responsible for these community dynamics by quantifying the species-specific contributions. We finally used the additive properties of our species contribution's expression to (iii) assess whether and how much contributions were distributed between particular categories (migratory and resident species) or taxonomic groups. The FBBS is a large scale and long term monitoring program in which skilled volunteer ornithologists count birds following a standardized protocol at the same site, year after year since 2001 (Jiguet et al., 2012). Species abundances were recorded inside 2 km × 2 km squares whose centroids were located within a 10 km radius around a locality specified by the volunteer. To improve the representation of the diversity of habitats countrywide, squares were randomly placed within the 10 km buffer (Veech et al., 2012). On each site, volunteers carried out 10 point counts (5 min each, separated by at least 300 m) twice per spring within three weeks around the pivotal date of May 8th to ensure the detection of both early and late breeders. Counts were repeated at approximately the same date between years (± 7 days) and at dawn (within 1–4 h after sunrise) by a unique observer. The maximum count per point for the two spring sessions was retained as an indication of point-level species abundance. We limited our study to sites belonging to the Mediterranean biogeographic domain because of the substantial climatic changes which occurred in this area during the period of study. Previous studies have demonstrated important changes in community structure and composition in this area during the period considered using this dataset (Gaüzère et al., 2015).

4.2. Analysis

We applied our community analysis framework to this dataset to describe the temporal variation in the CWM and CWV of the Species Thermal Index (STI, expressed in degree Celsius, see Devictor et al., 2008a,b). The STI is an integrative species characteristic representing the thermal preference of each bird species. It corresponds to the average temperature experienced by a species across its geographic range during the breeding season. STI values were computed from 0.5 by 0.5 degree temperature grids (April–July averages for the period 1950–2000; Worldclim data base, http://www.worldclim.org) coupled with species Western Palaearctic distributions at a 0.5 degree resolution from EBCC atlas of European breeding birds (Hagemeijer and Blair, 1997). The CWM of STI, (so-called Community Thermal Index) has been used to describe community reshuffling in response to climate change Devictor et al. (2012). We first described the temporal trends of both STI-based CWM and CWV. Then, we calculated the contribution of each species to the linear temporal trend of CWM and CWV. We finally proposed three different species contribution clustering (by taxonomy, by migrating behavior and by thermal originality, i.e. the difference between the STI of a species and the mean STI of the other species) to better characterize the highly contributing species.

First, we decomposed the CWM and CWV trends by orders. This taxonomical level regroups species with similar evolutionary history which generally leads to rather near ecological requirements, functions and behavior. Thus, their species might reveal similar responses to climate change. Moreover, some authors already suggested that vulnerability to climate change might exhibit phylogenetic signal (Thomas, 2008). While individual species contributions reflect the number of positive versus negative contributors, grouping these
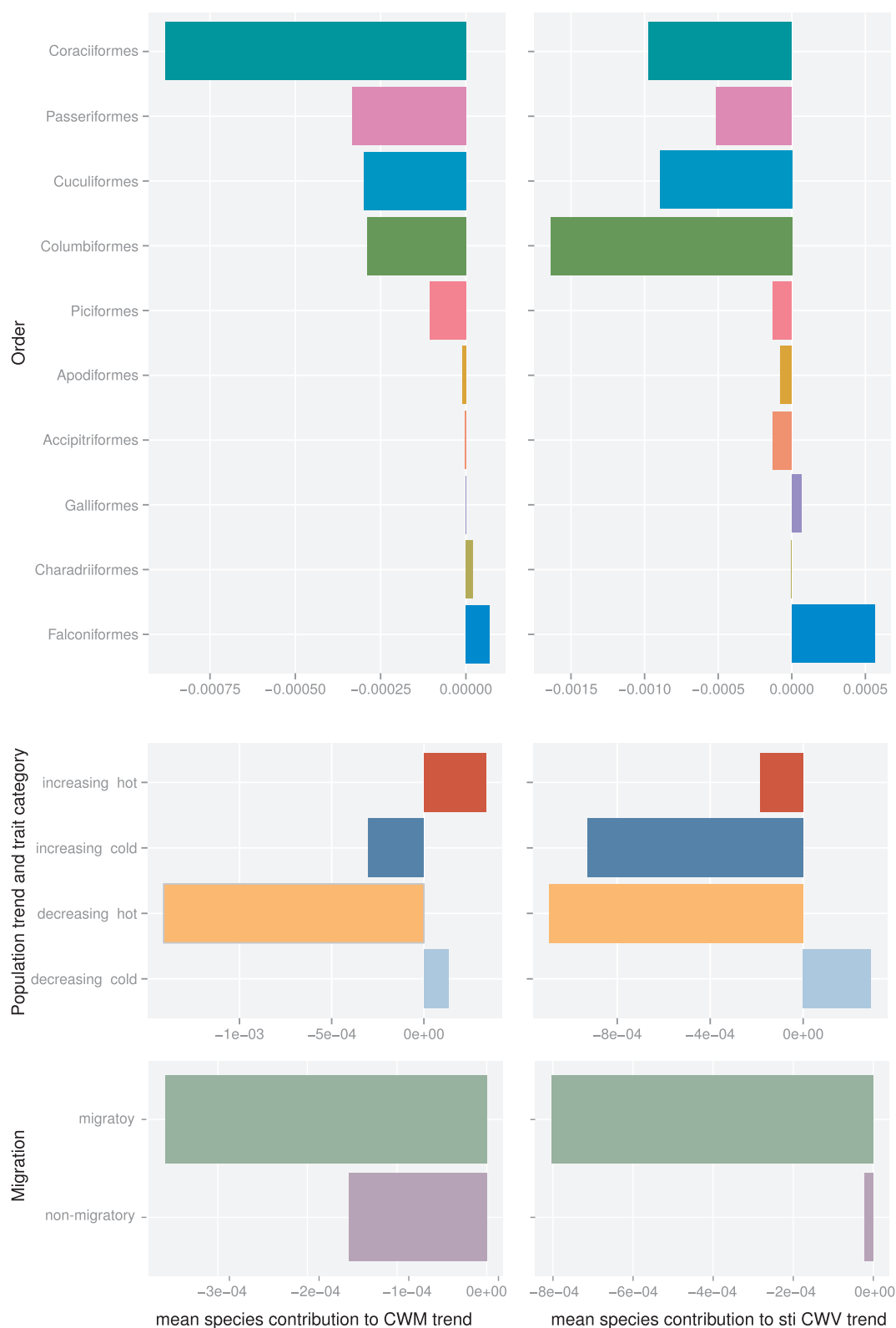
Fig. 4. Mean species contributions of common birds community weighted indexes of STI in the mediterranean region of France for the period 2001–2012. Top: Mean contribution by taxonomical order. Middle: Mean contribution by STI and population trend category: Red/orange: originally hot-dwelling species, blue/purple: originally cold-dwelling species. Bottom: Mean contributions for migratory and non migratory birds.

contributors according to their STI value could be even more informative to explain community changes. Therefore we secondly created four groups depicting the interplay between population trends of species and their STI values (increasing hot, increasing cold, decreasing

hot, decreasing cold; see Fig. 3). Third, we discretized species contributions between birds' migratory strategies. Following the hypothesis that species with stronger dispersal abilities are more likely to track environmental changes such as climate (Jiguet et al., 2007; Leroux and

Loreau, 2008), one can predict migrants birds to drive a large part of community dynamics facing global changes. All analyses were performed using the R software. We provide both R (s3cR) and python (s3c) packages with this paper to reproduce them.

4.3. Results

4.3.1. Temporal dynamics

The CWM of STI (also called Community Temperature Index, see Devictor et al., 2008b) of Mediterranean bird communities showed a steep linear decrease between 2001 and 2012 with a low year-to-year variation (linear model: -0.032 ± 0.004 °C. year^{-1}, $t = -6.762$, $df = 10$, $P < 0.001$) (Fig. 2) resulting from change in the relative proportion of warm (high STI) vs. cold (low STI) breeding range species within communities. This observation is in line with other studies on Mediterranean bird communities using the same approach and has been related to a sharp decrease in spring temperatures in this area during the same period (Gaüzère et al., 2015).

The CWV of STI similarly showed a linear decrease between 2001 and 2012 (linear model: -0.049 ± 0.008 °C. year^{-1}, $t = -5.652$, $df = 10$, $P < 0.001$). This decrease indicated a community level homogenization of STI arising from changes in the relative proportion of common vs. original STIs.

The close correlation between CWM and CWV (Pearson's test: $t = 11.887$, $df = 10$, $P < 0.001$) allows us to refine the interpretation of the CWM and CWV trends. Following the framework described in Fig. 1, we can infer that the community dynamics are mostly driven by the local extirpation of originally hot species (decrease in CWM and decrease in CWV).

4.3.2. Species contributions

Calculating species contributions to the trend in CWM (Fig. 3, top) revealed that species were contributing differentially, even if weak but significant correlations were observed when comparing the species contribution between CWM and CWV dynamics. Many species exhibited negligible contribution values (Fig. 3), indicating that only a few key contributor species shaped the trends in the two community indices. The taxonomic clustering of species contributions (Eq. (5)) allowed us to compute the average species contributions of each bird order represented in the Mediterranean domain. Our results showed that four orders (Coraciiformes, Cuculiformes, Columbiformes, Passeriformes) exhibited high average species contributions, whereas others (Galliformes, Charadriiformes, Apodiformes, Accipitriformes) were not contributing to the CWM and CWV dynamics. The Falconiformes were the only order substantially contributing against the community weighted indices trends.

The grouping of species contributions (Fig. 4) showed that the negative trend of the STI-based CWM is mainly due to hot-dwelling species experiencing negative temporal trends. The decrease in the variance of the STI seemed to be driven by both hot-dwelling species with a negative population trend (as conjectured from the CWM-CWV correlation) and cold-dwelling species with a positive population trend. Migratory species were stronger contributors to the negative community indices trends than non migratory species.

5. Discussion

Community Weighted Means (CWM) are simple and widespread indicators of the community composition. They have been used in a large range of studies across different natural systems and as an indicator of climate change impact on biodiversity by the European Environmental Agency (Marcus, 2010). However, little work has been done to bring those indices beyond coarse-grained community indicators (but see Princé and Zuckerberg, 2015).

Current CWM approaches are weakened by their inability to consider interspecific and intraspecific variances to community level

dynamics (Julliard et al., 2003; Hickling et al., 2006). Our work expands this framework by introducing a decomposition of their variation in species contributions, thereby linking community responses to species-specific dynamics and traits. Our work can be seen as the extension of what has been done on diversity indices. Indeed, Simpson's diversity index is essentially a CWM where the species-specific characteristic of interest considered is the very species relative abundance itself. In this context, the CWV is the equivalent of the community evenness measure (Hill, 1997). Overall, these additions provide new insights to interpret aforementioned community-level changes. Bridging the gap between species and community approaches therefore allows the testing of key ecological assumptions related to autecology or evolutionary history, which is crucial for community ecology and conservation biology. The documented community changes in French Mediterranean birds is a good illustration of this: between 2001 and 2012 an overall drop in spring-temperature triggered an important decrease in the CWM of the species thermal index. However further characterization of this phenomenon, particularly at lower integration levels, remained elusive. The substantial decrease of the realized thermal niche diversity, as measured by the associated Community Weighted Variance (CWV), is the result of an overall loss in relative originality of species' thermal preferences. At higher scale, this result suggests a jeopardization in the ability of communities to adjust their composition in response to further environmental change. Moreover, the strong correlation between Community Weighted Means and variance suggests that the change was driven by local extirpations (or decreasing local abundance) of particularly hot-dwelling species (i.e species carrying relatively hot and original thermal indices).

The decomposition of the community trend in species contributions corroborates these results and opens a novel range of questions. By allowing the aggregation of species trends, this method shows that migratory species are on average higher contributors to the Mediterranean bird communities thermal reshuffling. This result is in agreement with the hypothesis that species with larger ability to shift their distribution range are more likely to track brutal environmental changes.

However, the most commonly pointed out shortcoming of CWM is not addressed here: the difficulty to disentangle effects from climate change from confounding variable (e.g. interaction between land use modifications and climate change that would also influence the trait value, see Clavero et al., 2011; Barnagaud et al., 2012a; Barnagaud et al., 2013; Davey et al., 2013; Roth et al., 2014; Zografou et al., 2014). Ultimately, going beyond statistical correlation to causal explanations would require the use of controlled experimentation at community scale. Note however that a well designed study of species contribution can help to emphasize whether species with specific associations to particular habitats (e.g. forest specialists) are even more contributing to CWM or CWV calculated on thermal preferences (STI) than others.

Overall, the community weighted indexes (CWM and CWV) framework provides simple community indicators, rooted in the interaction milieu paradigm (McGill et al., 2006). It offers a simple univariate alternative to encompassing multitraits methods (e.g. hypervolumes as in Blonder et al., 2014). This simplicity allows for more straightforward interpretation. Thus, the selection of the trait used to apply the framework and evaluate the indices must be careful and in line with the ecological question asked. A first approach uses *specific indicator values* (e.g. Species thermal index or Ellenberg averaged values) defined at the species level that are naturally linked to environmental parameters (for instance in environmental calibration, see Ter et al., 1986). A second approach uses *functional traits* (such as body mass, lifespan, leaf area... see Violle et al., 2007) defined at the individual level (thus allowing the measure of intraspecific variability) are linked with evolutionary strategies (r/K) and ecological performances (productivity), or ecosystem functioning (Reiss et al., 2009). These indices are able to carry functional information (as opposed to species richness or evenness measures) while staying focused on the traits relevant to the phenomenon

studied (as opposed to more general functional diversity measures, see Villéger et al., 2008).

The recent rise of long term biodiversity (Dornelas et al., 2018) monitoring has revealed the high prevalence of nonlinear trends (e.g. Barnagaud et al., 2017). However, in its current form our decomposition of species contributions are exact only on linear trends fitted with ordinary least squares. This choice stems from the difficulty associated with the interpretation of species contributions to non-linear trends. It is, indeed, challenging to interpret a positive or negative contribution to a nonlinear trend including periods of linear increase and decrease. To deal with non-linear dynamics, we therefore advise to use contributions on well chosen linear segments of community dynamics. Such temporal breakpoints in diversity trends can be easily assessed using piecewise regression models (Muggeo, 2008).

Preliminary results in our bird dataset showed that the distribution of contributions are presenting a taxonomic structure, with some orders systematically associated with strong contributions values. A systematic study of the putative phylogenetic signal of contributions could lead to new insight on the evolutionary basis of community perturbation patterns.

Overall, computing species' contributions to community indicators changes is a simple and potentially powerful way to measure and interpret natural community changes.

Data accessibility

The following will be provided with the manuscript:

- STOC data for the mediterranean region for the period 2001–2012 (will be uploaded on Zenodo).
- s3c python package implementing the computation of CWI and contributions.
- s3cR R package implementing the computation of CWI and contributions.
- Scripts written with these packages and data that were used to produce the figures

Author contributions

All authors defined and designed the goal of the study. G.D. wrote the mathematical framework, P.G conducted the data-analysis. G.D and P.G led the writing in close association with V.D. and S.K. The authors declare having no conflict of interest.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.ecolind.2018.11.069.

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